Range Expansion of the Tree Swallow, Tachycineta bicolor (Passeriformes: Hirundinidae), in the Southeastern United States

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ABSTRACT—Since the late 1800s and early part of this century when the tree swallow, Tachycineta bicolor, was a peripheral and sporadic breeding species in the southeastern United States, its range has expanded considerably. The precise reasons for the range expansion of this and other swallows in the Southeast is unclear. Land clearing, impoundments and other land use patterns, the re-introduction of beavers (Castor canadensis), and the use of bluebird (Sialia sialis) boxes by swallows as nest sites appear to have facilitated the expansion. Several different corridors of dispersal are noted; North Carolina represents the current frontier of range expansion in the Southeast.

The 1957 edition of the American Ornithologists' Union Checklist (AOU 1957) stated that the breeding range of the tree swallow (now *Tachycineta bicolor*) extended south to northwestern Tennessee, northern West Virginia, Virginia, central Maryland, and northeastern Pennsylvania. At the turn of the century the species rarely nested as far south as southwestern Kentucky (Fig. 1). The breeding range has expanded considerably since the 1950s, but this change in distribution is not well documented. By the early 1980s the southern limits of distribution were defined as northeastern Louisiana, westcentral Mississippi, Tennessee, and North Carolina, but the tree swallow was "generally sporadic or irregular as a breeder east of the Rocky Mountain states and south of the upper Mississippi and Ohio Valleys, or along the Atlantic coast south of Massachusetts" (AOU 1983).

At least in parts of the Southeast, tree swallows are currently undergoing a rapid range expansion and indications are that they will become common and widespread throughout much of the area during the coming decades. This pattern of range expansion has already been exhibited by several other species of swallows in the Southeast. The majority of the information presented here is from North Carolina, which is the current frontier of range expansion in the Southeast.

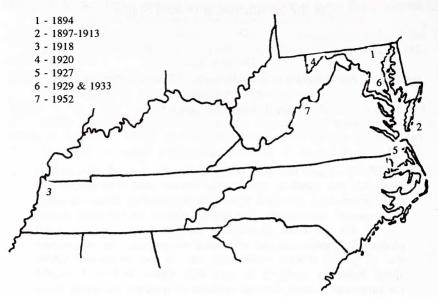


Fig. 1. Early isolated breeding records of tree swallows (*Tachycineta bicolor*) in the southeastern United States. See text for documentation sources.

METHODS

Information presented here is compiled from numerous published sources such as state bird journals and from unpublished records obtained from individuals and agencies monitoring bird distributions in the southeastern United States.

RESULTS

West Virginia—Hall (1983) notes that most West Virginia summer records are from the mountains where nests have been found near beaver ponds and other flooded sites. Definite nest records were given for Hampshire, Preston, Tucker, Randolph, and Pocahontas counties. Hall (1983) also reported nesting records outside the mountains from the McClintic Wildlife Station, Mason County (several occasions), at Belle, Kanawha County (1961), and Randolph County (1975). Additionally, there are summer sightings for Jefferson, Morgan, Pendleton, Greenbrier, Mercer, Wood, and Gilmer counties in West Virginia. These records indicate a considerable expansion since the 1957 AOU Checklist.

Maryland—Stewart and Robbins (1958) reported tree swallows as breeding commonly in the tidewater region of the southern Delmarva and as being uncommon or rare breeders in other tide-

water areas of Maryland's Coastal Plain. This species was first reported as breeding in this area in 1929 and 1933 (unpublished egg catalogue of E. J. Court; Court 1936), but based on Virginia records (see below) it was probably present some time before Court's report. A disjunct portion of the breeding range was also noted in the Allegheny Mountains (Garrett County) with five specific nesting localities listed (Stewart and Robbins 1958). Despite a moderate amount of fieldwork in western Maryland early in this century, the first report of mountain nesting was not until 1920 (Eifrig 1920) with subsequent records in 1936 (Brooks 1936). The earliest documented nesting in Maryland was 1894 (W. H. Fisher; in Stewart and Robbins 1958). Although it is not known when tree swallows first started nesting in Maryland, it was likely just before the turn of the century. The 1894 record is for Baltimore County and is probably from Dulaney Valley north of Towson, where Fisher did most of his fieldwork (Lee 1988). Interestingly, this area was not considered part of the tree swallow's range in 1958. In 1968 the distribution was essentially unchanged (Robbins and Van Velzen 1968). Since then, however, the species has expanded throughout the state. It is still most numerous in the mountains and in tidewater areas. Tree swallows are now locally common nesters in the Maryland Piedmont (Maryland Breeding Bird Atlas data). Statewide they were found in 393 of the 1,256 Atlas blocks (31.2%), and they were found in every county in the state (C. S. Robbins, personal communication). Colonization of most areas in Maryland seems to be dependent on the species ability to nest in bluebird boxes.

Kentucky—Despite the state's location in relation to the historic range of tree swallows (southern Illinois 1889, Missouri 1894, and Tennessee 1918), the species was essentially unknown as a breeding bird in Kentucky even by the mid-1960s (Mengel 1965). The only record for the state before the 1960s is from 1889 to 1925 when Pindar noted that tree swallows were present in Fulton County in the summer. This county is in the extreme western tip of the state along the Mississippi River and just north of Reelfoot Lake, the site of the first record for Tennessee (Pindar 1889, 1925). Mengel (1965) visited this area between 1941 and 1951 and, although he noted favorable habitat, he did not locate nesting birds. Breeding was again noted in 1905 in the Cumberland River Valley (Lyon County at Long Run Park in Jefferson County) in 1975 (Monroe et al. 1988). The species is now recorded as nesting in scattered localities throughout the state. Its nesting is mostly along edges of lakes and rivers where there are many dead trees, and recently the species has been found using nest boxes (Monroe et al. 1988).

Virginia—In the early part of this century, Bailey (1913) recorded the tree swallow as nesting only on the lower Delmarva portion of Virginia where it bred mostly on islands. Murray (1952) summarized the historical nesting status in Virginia as follows: "There is one nesting record for Princess Ann County, June 15, 1927, upper end of Back Bay, Lewis; and one for Aylett, King William County, no date (Auk 14, 408). Palmer found a nest with young on Smith Island, June 10, 1897; and reports one with eggs, May 1894 (Auk 14, 408). Brooks states that it is a 'fairly common summer resident at the higher elevations at least in Highland County (Raven 6, 11–12, 2)."

By the late 1970s Larner et al. (1979) noted that the tree swallow was locally common in the Virginia portion of the Delmarva Peninsula and rare elsewhere in the Coastal Plain. In the Piedmont it was a rare and local summer resident, and the first breeding record "in recent years" was recorded in Madison County in 1976. Larner et al. (1979) reported records in the mountains from Augusta, Highland, Russell, and Tazewell counties. In the last decade this species has greatly expanded its range in Virginia with confirmed nesting records in 34 counties (65+ sites) throughout the state and expected or presumed nesting in at least 18 additional counties (Sue Ridd, personal communication 1988; Virginia Breeding Bird Atlas).

Tennessee—The first nest was discovered at Reelfoot Lake, Tennessee, on 22 May 1918 (Ganier 1964) but from that time until 1968 no additional nests were reported; there was only one other observation of these swallows during the breeding season. Olson (1968) found an active nest at Norris Lake in Anderson County in 1968, and the same year Gray (1968) found a nest at Monsanto Ponds in Maury County. The early records were from the western part of the state adjacent to the Mississippi River. Since 1968 nests have been reported in Tennessee almost annually. Nicholson and Pitts (1982) summarized the distribution of nesting in Tennessee, noting that in recent years tree swallows have nested throughout the state.

North Carolina—In North Carolina tree swallows were first reported nesting in 1979 in the extreme northwestern corner of the state (LeGrand and Potter 1980). The nest was in an abandoned woodpecker cavity along the New River in Ashe County (elevation 9,100 m). The second record was nearly 192 km southeast of this site, and 2.4 km north of Asheville in Buncombe County near the French Broad River (elevation 600 m) in 1981 (Duyck 1981). In the subsequent decade the breeding range has expanded considerably.

Breeding Bird Atlas volunteers in North Carolina found tree swallows nesting in the mountains in the southwestern part of the state in Transylvania County (four locations) and in Henderson County. Nesting was recorded in 1988 and 1989 and will probably continue in the future. In 1988 and 1989 a pair nested in a purple martin (*Progne subis*) gourd in Cowee Valley, Macon County, and in 1990 a pair nested in a bluebird box near Piney Creek, Alleghany County (Chat 55:64–65). The Piedmont birds were seen nesting in woodpecker cavities in trees killed during flooding to create Jordan Lake in Chatham County in 1988. A nesting pair was found in Vance County in 1990. To date these are the only confirmed nesting birds in the Piedmont. In the Coastal Plain, tree swallows were found nesting in eight locations in Currituck County (1989–90), and were seen during the nesting season in Pamlico County (1988) and along the lower Cape Fear River in Brunswick County (1990). In the Coastal Plain pairs of tree swallows used bluebird boxes and natural cavities in trees killed by impoundment and where natural flooding occurred along rivers and in salt marshes.

DISCUSSION

Although present day land-use patterns provide fields and other open areas suitable for swallow foraging, this alone does not account for the current, explosive range expansion because land clearing was widespread in the Southeast by the early 1800s. Nest sites are critical, and the same land-clearing patterns that provide open areas can also eliminate snags and other potential cavity-nest sites. The elimination of beavers from most of the Southeast at the turn of the century eliminated the potential for natural snags in areas impounded by beavers. Dead trees resulting from flooding in tidewater areas and adjacent salt marshes seem to have provided a natural dispersal route in coastal areas. Therefore it is interesting, and not easy to explain, that, despite the availability of natural habitat, tree swallows have only recently (since 1913 in Virginia; late 1980s in North Carolina) expanded in tidewater areas. It is to be expected that coastal tree swallows will also follow river systems inland and make use of dead trees in impoundments and beaver ponds in the Coastal Plain.

Phenology—Tree swallows are relatively early to late spring and early to late fall migrants, making it difficult to distinguish resident breeding birds from migrants. In Currituck County, North Carolina, in June 1990 I observed resident birds using cavities before, during, and after a fairly extensive northern migration of large numbers of transients. Nicholson and Pitts (1982) noted tree swallows at Reelfoot Lake, Tennessee, by mid-March, and territorial birds by late April when northbound migrants were still present. Southward migration in the southeastern United States begins in early July (Nicholson and Pitts

1982, personal observations). Major fall migration occurs in October, and birds winter in much of the Southeast, particularly along coastal areas.

Nesting dates in the Southeast range from 12 May to 3 July with no indication that pairs at southern latitudes nest any earlier than those to the north. The earliest recorded egg date, for example, is from Maryland (see below). Birds reported in from North Carolina (NCSM records) nested from early May through mid-June. The following is a list of nesting dates for the Southeast: 4 May-21 June, nesting activity (15-20 May eggs laid), North Carolina (Duyck 1981); 6 June, adult feeds fledglings, Tennessee (Williams 1976); 9 June, adult feeding young, Tennessee (Nicholson and Pitts 1982); 16 June, adult and fledged young, Tennessee (Nicholson and Pitts 1982); 9 June, adult at nest, North Carolina (Chat 44:9); 11 June, young birds being fed, North Carolina (Chat 44:9); early July, feeding young, Tennessee (Nicholson and Pitts 1982); early May to mid-July (egg dates 24 April-5 July, nestling 20 May-27 July), Maryland (based on 320 Maryland nest records, C. S. Robbins, personal communication).

Pattern of Range Expansion—Apparently the expansion of nesting into the outer Coastal Plain of Maryland, Virginia, and North Carolina, the southern Appalachians, Maryland, to North Carolina, and the Piedmont regions of these states occurred independently (Fig. 2). Sites along major rivers and those adjacent to cleared agricultural areas were the first to be colonized (i.e., 1889–1918 Mississippi River low-lands). Colonization occurred rather rapidly in the mountains (1920–36 Maryland, by 1929 in Virginia, and northern West Virginia pre-1957), and accelerated in the last decade (northern North Carolina in 1979 to southwestern North Carolina by 1988). Many of these sites were along rivers in the Mississippi basin.

In the Coastal Plain the species was nesting on the Delmarva as early as 1897, but was not common or widespread even by the 1950s and did not become so until the 1970s. Breeding individuals did not invade northeastern North Carolina until the late 1980s.

Their occurrence in the Piedmont seems sporadic. The earliest Piedmont record from the Southeast and Atlantic states is 1894 (Maryland), but the birds did not become established. Piedmont nesting was not documented until 1961 (West Virginia) and 1976 (Virginia) and was not widespread until the 1980s (Maryland and Virginia). This swallow is still uncommon the North Carolina Piedmont where it is known from only two sites. West of the Appalachians, this species had a similar history in Tennessee where the first nest was reported in 1918 with no new records until the second half of the 20th Century. Yet the species was nesting throughout Tennessee by 1982.

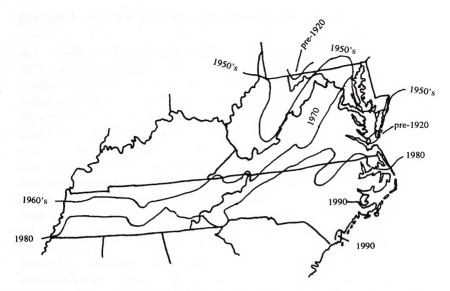


Fig. 2. The expanding breeding distribution of the tree swallow (*Tachycineta bicolor*) in the southeastern United States (1894-1991).

Possible Explanation for Range Expansion—Tree swallows might now be imprinted on bluebird boxes as nesting sites, and this imprinting possibly has allowed them to expand their range into areas where the lack of natural cavities would otherwise inhibit nesting.

Plasticity in food habits may also be important in the range expansion of this swallow. Lee and Franz (1972) reported on a premigration staging flock of several thousand tree swallows feeding over a cornfield on the eastern shore of Maryland. Examination of the stomachs of a dozen birds revealed corn flea beetles (*Chaetocnema pulicaria*). No other food items were found. Food items were counted in one stomach, and 170 corn flea beetles were found. Although I am not aware of other direct observations of tree swallows benefiting from agriculture or agricultural pests, at the minimum the clearing of land for agricultural purposes has created foraging areas not available in the precolonial period.

Several nesting sites are associated with man-made lakes and large impoundments constructed for waterfowl. Many hardwood trees killed by floodwaters contain cavities made by woodpeckers that provide multiple nest sites where the swallows form small colonies of a dozen or more pairs. Although the beaver was reintroduced by various state wildlife agencies and has made an explosive come-back, this generally precedes the period of range expansion of tree swallows outlined

here (see Bonwil and Owens 1939, Mansuetti 1950, Lee 1988, and Lee et al. 1982).

Similar Range Expansion of Other Species of Swallows—The relatively rapid range expansion parallels the changing distribution of other swallows in the Southeast. The barn swallow's (Hirundo rustica) breeding range was largely to the north of North Carolina before 1942 (Pearson et al. 1942), but it bred locally in the mountains in the northwestern corner of the state and along the coast. The range expansion in the state was undocumented. By 1975 the species was colonizing the outer Coastal Plain in southeastern North Carolina, and today it occurs statewide (personal observation). Although they nest in barns and under docks, the main factor allowing dispersal seems to be the replacement of wooden bridges with concrete ones throughout the state (1960s-70s); the swallows use the concrete bridges for nest substrate.

At the beginning of this century cliff swallows (Hirundo pyrrhonota) were only transients in North Carolina. In 1967 they were reported nesting in the state, and by 1983 they had expanded their range in the Piedmont to Greensboro, Guilford County (Hendrickson 1984). They had previously been reported nesting at other Piedmont sites, all around reservoirs (Lake Cammack, Hyco Reservoir, McGehee's Mill, and Jordan Lake). They also nest at Falls Lake, Wake County (NCSM records, 1989). Like tree swallows, this species did not simply expand its range from north to south or from the west to the east as one might expect. They colonized scattered sites in the Piedmont and later colonized suitable adjacent sites. McConnell (1981) first reported nesting in the Mountains of North Carolina and noted a preference for reservoir dams as nesting sites. This range expansion, which started in the mid-1960s, also includes the Piedmont regions of Virginia, South Carolina, and Georgia, and in southcentral Florida (summary in Grant and Quay 1977).

Platania and Clark (1981) discuss the 1960-80 range expansion of northern rough-winged swallows (Stelgidopteryx ruficollis) in the North Carolina Coastal Plain and mapped the known breeding distribution of the species in the state. They also reported nesting season records of bank swallows (Riparia riparia) from Roanoke Island, Dare County, but a colony apparently never formed there. Bank swallows have nested sporadically in North Carolina. Earlier records were available from 1926 to 1940 in Henderson County (Nicholson 1951, Pickens 1954). Snavely (1978) reported a colony in Wilkes County that was present from 1977 to 1978. This was the first recent nesting record for the state, but the colony has since died out. Subsequently, Lee and Hendrickson (personal observations) found a nesting colony near

Linville in the Mountains of North Carolina in 1991. All North Carolina nest sites are in artificial banks made by large earth-moving equipment.

Thus, it appears that current land use practices have provided open foraging habitats, and various man-made structures and land modifications have provided suitable artificial nest sites, thus allowing various species of swallows to expand their breeding range in the Southeast.

CONCLUSIONS

Like other species of swallows, the tree swallow has expanded its range considerably since the late 1800s. Earliest records show the species to be a peripheral breeding species in the southeastern United States, and nesting records are sporadically distributed both geographically and temporally (Fig. 1). Range expansion appeared to be gradual through the 1960s and then explosive from the 1970s to the present as the birds populated the Piedmont of Maryland, Virginia, and portions of North Carolina (Fig. 2). The species expansion in the mountains, Mississippi basin, and Coastal Plain occurred at different rates. Overall the species has spread south over 600 km in this century with approximately 220 km (35%) of this expansion occurring in the last decade. Although various factors such as land clearing were obviously necessary for the range expansion to occur, the timing of these changes in land use does not appear to correspond directly with the expansion in range.

Although land clearing probably benefited all species of swallows nesting in the Southeast, the change of distribution is also related to availability of nesting sites. Thus, the northern rough-winged swallow, the species with the least demanding requirements for nesting sites, was the first to expand its range. Barn swallows followed, expanding into the Piedmont and Coastal Plain as wooden bridges were replaced with concrete ones. Cliff swallows have nested in North Carolina only since the 1960s, and their current distribution is discontinuous and dependent on the large reservoirs constructed in the latter part of this century. Tree swallows expanded their range with the re-introduction of beavers and after their adoption of nest boxes. The bank swallow, which has the most restricted distribution, relies on exposed banks that are sporadically distributed and often not continuously available because of erosion and invading plant communities.

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